Chemical Senses and Flavour Volume 4 Number 1 1979

Taste quality changes as a function of salt concentration in single human taste papillae*

Armand V. Cardello**

University of Massachusetts, Amherst, MA 01002, USA

(Received May 1978; accepted November 1978)

Abstract. A series of experiments were performed to determine whether concentration-dependent taste quality changes occur in simple salt solutions when presentation of these solutions is restricted to single fungiform taste papillae. Preliminary experiments, using small area, dorsal tongue stimulation, revealed the presence of a sour-salty confusion in response to NaCl and HCl stimulation. This confusion was found to be greater at higher concentrations and was affected by a pre-rinse. Taste quality changes as a function of solution concentration for NaCl, KCl, and LiCl stimulation of single papillae were found to parallel those found previously with whole-mouth stimulation, although the sour component was greater at high concentrations, reflecting the effect of the previously identified sour-salty confusion. The data are discussed within the context of Dzendolet's (1968) physicochemical theory of taste quality changes in salts.

Introduction

Taste quality changes as a function of the concentration of simple salts have been reported previously (Hober & Kiesow, 1898; Renquist, 1919; Dzendolet & Meiselman, 1967; Cardello & Murphy, 1977). The results of these studies indicate that both concentration-dependent physicochemical changes in these solutions, as well as water tastes resulting from adaptation to salivary constituents, combine to affect the taste quality of inorganic salts at low concentrations (Cardello & Murphy, 1977).

Dzendolet (1968) has put forth a theory which accounts for these taste quality changes within the context of his proton-acceptor theory of sweet taste. According to this theory, the localized hydrolysis which occurs in dilute salt solutions can produce a chemical structure in which the cations of the salt are surrounded by a shield of hydroxyl ions (Harned & Owen, 1950, pg. 385). Since hydroxyl ions are proton acceptors, the sweet taste reported at low concentrations of these salts is predicted. At high concentrations other physicochemical changes occur which account for the reported taste qualities of these solutions. One such change which can account for the sour taste of some salts at intermediate concentrations results from increased hydrolysis at these concentrations. This hydrolysis produces hydrogen ions in excess of the number which can be neutralized by salivary constituents. The resulting stimulation of "sour" receptors overcomes the previous stimulation of "sweet" receptors through a process of inhibition. At still higher concentrations the effect of the anion exceeds the threshold for the salty quality and

* This research was conducted as part of a thesis submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy at the University of Massachusetts/Amherst.

** Current address: Behavioral Sciences Division, Food Sciences Laboratory, US Army Natick Research and Development Command, Natick, MA 01760, USA produces inhibition of previously stimulated receptors (Dzendolet & Meiselman, 1967).

The inhibitory effect as originally proposed by Dzendolet is assumed to occur between quality-specific papillae, and one prediction that can be made from his theory is that taste quality changes will *not* occur as a function of the concentration of simple salt solutions when stimulation is restricted to a single papilla. Recent studies of single papilla response characteristics (Harper, Jay, and Erickson, 1966; McCutcheon and Saunders, 1972; Bealer and Smith, 1975; Cardello, 1978) have effectively ruled-out the notion of specificity in fungiform papillae. However, the question of whether taste quality changes occur as a function of solution concentration in salts, when stimulation is restricted to a single papilla, is still unanswered. The only published data that bear on this question are those of McCutcheon and Saunders (1972). They reported that "sour" was the most common taste quality given by their subjects to describe the taste of 0.4 M NaCl. However, McCutcheon & Saunders (1972) also found repeated quality reports of "salty" in response to presentations of 0.1 M citric acid. Harper, et al. (1966) reported similar "inappropriate" quality responses for other compounds, as did Collings (1973) for small area stimulation with saturated filter paper, suggesting that the sour taste of NaCl reported by McCutcheon & Saunders (1972) may reflect a reduced discriminability of taste qualities under conditions of small area stimulation, rather than a concentration-dependent quality effect.

Experiment I

Since single papilla testing involves stimulation of an extremely small area of the dorsal surface of the extended tongue, a preliminary experiment was conducted to assess the effect of small-area dorsal-tongue stimulation on taste quality identification. Stimulation was *not* restricted to a single papilla in this experiment, in order that the general effect of small-area stimulation could be compared with that of the whole-mouth.

Method

Subjects. Three females and one male, between the ages of 20 and 24 served as subjects. All were students at the University of Massachusetts/Amherst or area residents. Each was screened prior to participation by the method reported in Meiselman & Dzendolet (1967). None of the subjects smoked and none were taking medication at the time of participation.

Stimuli. Test solutions were 200 mM sucrose, 20 mM HCl (pH = 1.70), 1mM quinine sulfate and 2000 mM NaCl. All solutions were mixed with reagent grade chemicals and distilled water within 72 hours of their use. All were stored in glass containers at 25°C, with the exception of sucrose which was stored at 4°C. During testing all solutions were at room temperature.

Procedures. The subject was seated at a table adjoining a sink and his/her head positioned in a metal head restraint. At the start of each trial the subject extended his/her tongue to expose the anterior 3 cm. A 45-second period then elapsed during which time excess saliva was allowed to dry from the tongue surface. The latter procedure was employed to mimic the conditions required for single papilla stimulation. Following this drying period one of the four test solutions was presented to the dorsal surface of the tongue with a 1.0 ml glass medicine dropper. The volume of the solution droplet was 0.02 ml and it stimulated an area of approximately 50 mm^2 on the tongue surface. Placement of droplets was quasi-random across the surface of the tongue with an equal number of droplets of each solution presented to each quadrant of exposed surface. Each test solution was presented eight times to each subject.

After presentation of the test solution, subjects made two judgements of its taste quality. The first was made immediately after presentation of the stimulus, while the tongue was still in an extended position and the stimulus remained within a small circumscribed area on the dorsal tongue surface. The available responses were those of "sweet", "salty", "sour", "bitter", "indistinct or vague", and "no taste". Responses were made by placing the appropriate side of a small, labelled cube face-up on the experimental table. After marking this first quality judgement the subject retracted his/her tongue, moved the solution around with the tongue, causing it to distribute over the whole mouth, and then made a second quality judgement. The subject then rinsed with distilled water, expectorated, and awaited the next trial. An interstimulus interval of two minutes was maintained.

Results

The data were plotted as histograms. Figure 1 shows the percentages of taste quality responses to each solution under the two modes of stimulation. It is clear from these data that for all four solutions the percentage of "indistinct or vague' and "no taste" responses are lower in the "whole-mouth" condition than in the "dorsal tongue only" condition, indicating a difference in sensitivity between the two conditions. However, in addition, there are frequent inappropriate quality responses for both HCl and NaCl in the "dorsal tongue only" condition. Such misidentification of characteristic qualities is minimal in the "whole mouth" condition, and does not occur in any condition for sucrose or quinine sulfate. It can be seen from Figure 1 that the misidentifications are those of calling HCl "salty" and NaCl "sour".

Discussion

Considering the dorsal tongue data first, the fact that the concentrations of HCl and NaCl were high and that inappropriate responses to these compounds were non-random indicate that simple guessing alone cannot account for these data. Secondly, the fact that these inappropriate responses were not observed in the whole mouth condition, suggests that this pattern of responding is peculiar to some aspect of small area, anterior dorsal tongue stimulation. It is unlikely that the sequential procedure for affecting dorsal tongue and whole mouth stimulation is responsible for the improved discrimination in the whole mouth condition, since subjects could maintain their tongue in an extended position for up to 90 seconds with the stimulating solution on their tongue, but with no change in its taste quality or emergence of a taste quality that was not initially present. However, immediately upon retracting his/her tongue, the appropriate taste quality would be perceived. If

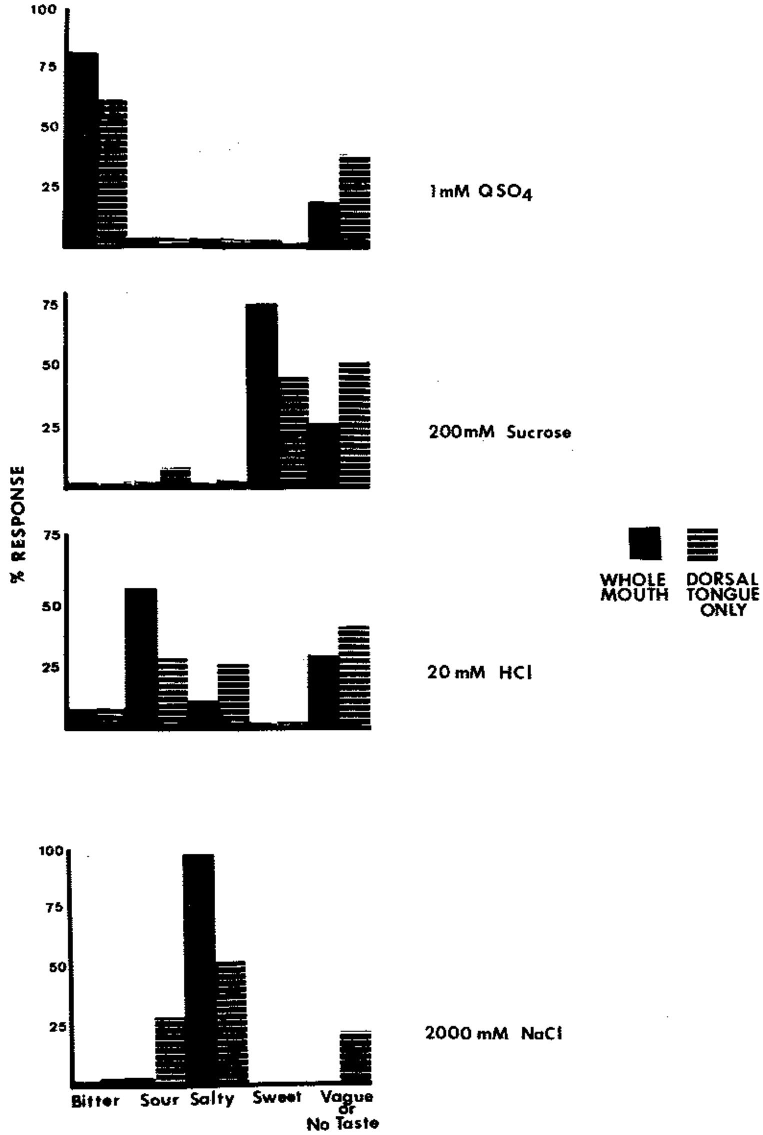

Fig.1 Histogram of the percentages of taste quality responses to small area, dorsal tongue and whole mouth stimulation.

the improved responding was due to an increased duration of stimulation resulting from the sequential procedure, then the appropriate taste quality of these compounds would also be expected to emerge when the stimulus was allowed to remain for long periods on the extended tongue. The fact that they did not, is evidence of an actual difference in discrimination between the two conditions and suggests the existence of a physiological or psychological "confusion" of the sour and salty qualities in the dorsal tongue condition.

A sour-salty confusion has not been extensively reported in the literature, as has the common sour-bitter confusion (Meiselman & Dzendolet, 1967; Robinson, 1970; Gregson & Baker, 1973; McAuliffe & Meiselman, 1974). However, von Skramlik (1926) and Moncrieff (1967, p. 487) have both presented anectodotal evidence in support of such a confusion. Similarly, much of von Bekesy's research has demonstrated an integral relationship between these two taste qualities (von Bekesy, 1964, a, b, 1965). These earlier lines of evidence, in combination with the data from Experiment I, required that a more detailed examination of quality responding to HCl and NaCl under conditions of small-area dorsal tongue stimulation be conducted before an adequate analysis could be made of single papilla quality responses to salts.

Three questions presented themselves: 1) Is the sour-salty confusion peculiar to high concentrations of HCl and NaCl? 2) Does the presence vs. absence of saliva affect the confusion? and 3) Is cooling and/or drying of the tongue surface in the dorsal tongue condition responsible for the confusion?

Experiment II

Method

Subjects. Subjects were the same as in Experiment I.

Stimuli. Concentrations were chosen to encompass the range in which both NaCl and HCl acquired a "stinging" quality in pilot tests. These concentrations were 10, 15, 20, 25, 30, and 40 mM HCl (pH = 1.96, 1.82, 1.70, 1.60, 1.52, 1.40) and 500, 1000, 1500, 2000, 2500, 3000, and 3500 mM NaCl.

Procedure. Prior to each trial, the subject extended his tongue in the same manner as in Experiment I. Upon instruction, the subject either rinsed his tongue with distilled water from a plastic squeeze bottle or did nothing. A 0.02 ml droplet of solution was then immediately presented, in the manner described previously. Subjects chose from the same quality descriptors as before and made responses in a similar manner. After responding, the subject rinsed his/her tongue, retracted it, and awaited the next trial. A three minute ISI was employed.

Whether or not the subject rinsed prior to presentation of the stimulus was random from trial to trial, as was the order of presentation of solutions. Each solution was presented 12 times under both the "rinse" and "no rinse" conditions.

Results

Grouped percentages of salty and sour responses to each solution are plotted in Figure 2. Responses other than sour or salty were minimal across subjects and solutions, totalling 7%. Most of these responses were either "no taste" or "indistinct or vague", reported at low concentrations in both the "rinse" and "no rinse" conditions. Two percent of the total were bitter responses given to various concentrations of HCl by two of the subjects.

The solid lines in Figure 2 represent responses in the "no rinse" condition, while the broken lines represent responses in the "rinse" condition. It is clear from these data that a confusion occurs at all concentrations, for both compounds, and in both

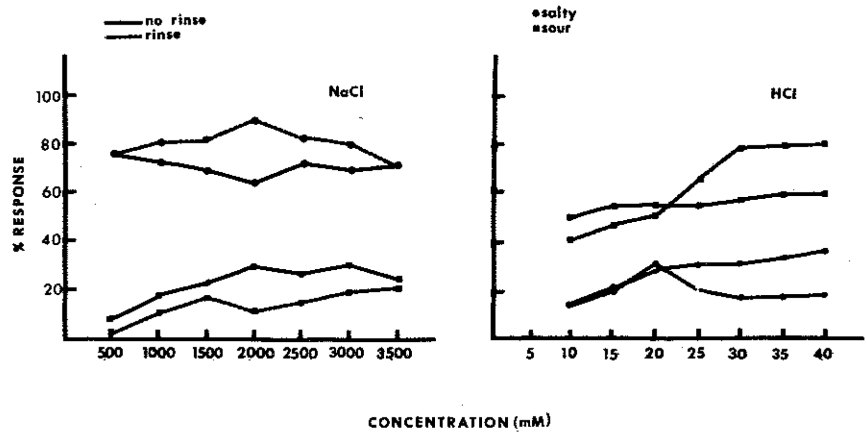

Fig.2 Plot of the percentages of sour and salty quality reports as a function of concentration of NaCl and HCl.

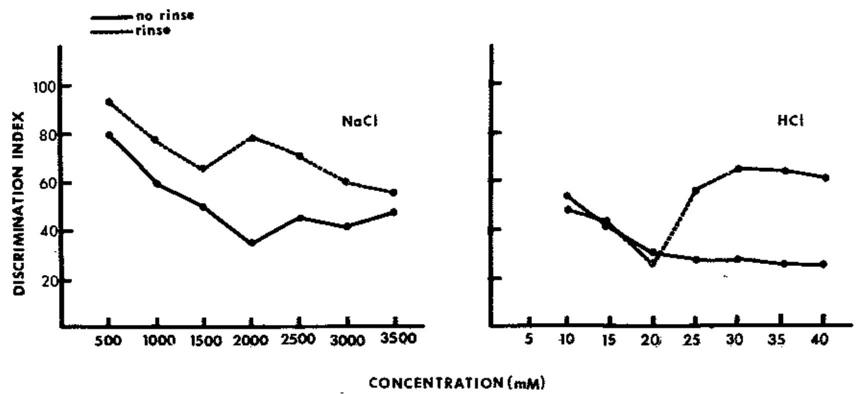

Fig.3 Plot of the "discrimination index" for "sour-salty" confusion as a function of the concentration of NaCl and HCl.

the "rinse" and "no rinse" conditions.

In order to assess the degree of confusion as a function of concentration and rinse condition, a "discrimination index" was calculated and the data replotted in Figure 3. The "discrimination index" of Figure 3 is defined as the ratio of the difference between the number of sour and the number of salty responses, compared to the total number of sour and salty responses given at each concentration, multiplied by 100. Thus, an index of 100 indicates complete discrimination between the two qualities, while an index of 0 indicates complete confusion of the qualities.

As is evident from Figure 3, there is a decrease in discriminability (increase in confusion) with increasing concentrations of NaCl and HCl in the "no rinse" conditions. For NaCl, the "rinse" condition shows a similar decrease in discriminability with increasing concentration, but the absolute level of discrimination is greater at all concentrations than in the "no rinse" condition. At low concentrations of HCl the confusion in the "rinse" condition is no different than that in the "no rinse" condition. However, at higher concentrations, the "rinse" condition shows a marked increase in discrimination (decrease in confusion) over that of the "no rinse" condition.

Discussion

Since the tongue was not dried in this experiment, yet the sour-salty confusion is as prevalent in these data as in the data of Experiment I, it may be concluded that cooling and/or drying of the tongue by evaporation does not contribute significantly to the confusion. The fact that the confusion increases with concentration supports a notion that the trigeminal component of taste may be an important contributing factor. Abrahams, Krakauer, and Dallenbach (1937), Holway and Hurvich (1937), McFadden (1937) and Hunt, DuBose and Meiselman (1978) have all reported strong tactile sensations for NaCl concentrations above 1600 mM. Moncrieff (1967) has reported similar tactile sensations for high concentrations of acids and has suggested that the "confusion between salt and sour tastes on the one hand and chemical irritants on the other" may be the reason for "the nineteenth century reluctance to recognize more than two tastes — those of sweet and bitter". More recently, O'Mahony (1973) has attributed the fact that high concentrations of NaCl sometimes taste sour or bitter to the unpleasant "hedonic tone" of these solutions. The reduction in confusion found throughout the concentration range for NaCl in the rinse condition of this study (Figs. 2 & 3) is consistent with findings that water-rinsing reduces NaCl recognition thresholds (O'Mahony, 1973; O'Mahony and Godman, 1974) and that taste profiles for NaCl have a greater salty component when preceded by a water rinse rather than by an adapting concentration of NaCl (McBurney, 1969; McBurney and Bartoshuk, 1973). The similar reduction in confusion with rinsing at high concentrations of HCl may reflect the important buffering action of saliva, particularly in response to concentrated acid solutions that possess a tactile component. The loss of such salivary buffering action in the rinse condition may facilitate discrimination of the trigeminal character of the acid stimulus.

Experiment III

Taste quality responses as a function of concentration for three inorganic salts were investigated within the context of a broader examination of psychophysical response characteristics of single human fungiform papillae.

Method

Subject, Apparatus, Stimuli. Subjects were 2 males and 2 females between the ages of 18 and 25. The apparatus consisted of a series of disposable plastic 1 ml tuberculin syringes, fitted with 33-gauge blunt stainless-steel hypodermic needles. Solution droplets were presented to the dorsal surface of single fungiform papillae with the aid of a dissecting microscope. (See Cardello (1978) for a detailed description of the apparatus and stimulating procedures.)

Salt solutions appear in Table I. In light of the observed confusions between salts and acids in Experiments I and II, an analysis of single papilla responses to acid solutions is of importance to the interpretation of the salt data. Thus, the acid

Table I. Salt and Acid Solutions Used in Experiment III

Salts			*Acids*	
NaCl	LiCl	KCl	HCl (pH)	Citric Acid (pH)
5000	5000	3500	50 (3.60)	500 (1.66)
3500	3500	2000	40 (1.40)	250 (1.83)
2000	2000	1000	30 (1.52)	100 (2.06)
1000	1000	500	20 (1.70)	50 (2.24)
500	500	250	10 (2.00)	20 (2.45)
250	250	100	5 (2.30)	10 (2.62)
100	100	40	1 (3.00)	5 (2.81)
40	40	10	0.5 (3.30)	2.5 (2.98)
10	10	5	0.25 (3.60)	1.0 (3.20)
5	2.5		0.1 (4.00)	0.5 (3.36)
2.5	2.5			0.25 (3.53)

Note: All solution concentrations are expressed in millimoles (mM)

solutions used in this study also appear in Table I. All solutions were prepared with reagent grade chemicals and mixed with distilled water. All were tested at room temperature (25°C).

Procedure. The subject sat at a table adjacent to a sink. At the start of each trial the subject extended his/her tongue to expose the anterior 3 cm. A 45-second period then elapsed during which time excess saliva was allowed to evaporate from the tongue surface. Following this drying period a 0.05 μl droplet of solution was presented to the dorsal surface of a chemically responsive fungiform papilla. Papillae were tested quasi-randomly, with successive presentations to the same papilla separated by at least five presentations to other papillae.

After presentation of the stimulus, the subject judged its taste quality while his/her tongue was still in an extended position. Taste quality choices included salty, sweet, sour, bitter, no taste, indistinct or vague, and complicated taste, and were made with a labeled response cube. The "indistinct or vague" category was used to describe weak taste sensations that could not be identified, while the "complicated taste" category was used to describe strong taste sensations that could not be classified as one of the four basic tastes.

After making each judgement, the subject rinsed his/her tongue with distilled water, retracted it, and awaited the next trial. A two-minute interstimulus interval was employed. Solutions were presented by a modified method of constant stimuli (see Cardello, 1979) and each solution was presented twice to each of 10 fungiform papillae in each subject.

Results

Figures 4 - 6 show the percentage of quality responses at each concentration of NaCl, LiCl and KCl. Data were collapsed across papillae and subjects, because the number of responses for individual papillae and/or subjects were too few at some concentrations to be considered separately.

At their lowest concentrations NaCl and KCl are sweet. LiCl also shows a greater percentage of sweet responses at lower concentations, but a strong bitter component

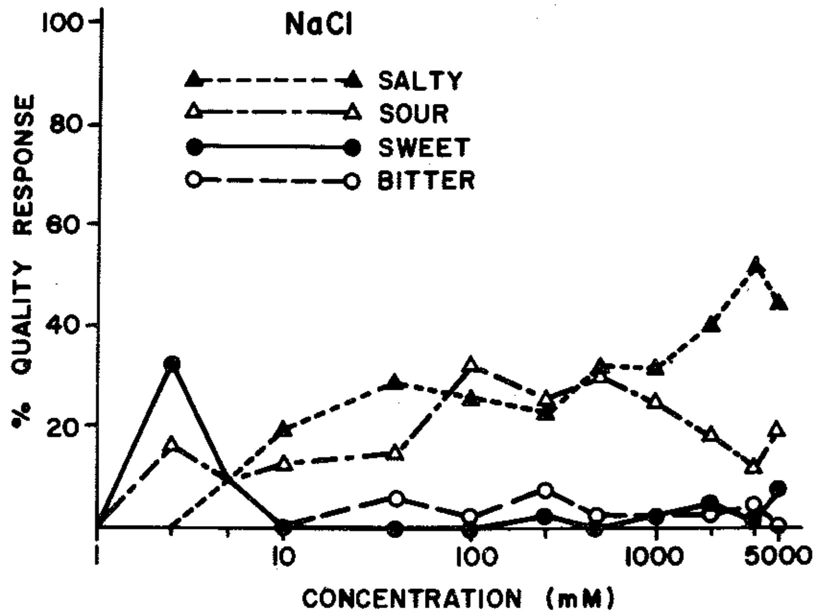

Fig.4 Percentage of each quality response as a function of concentration of NaCl.

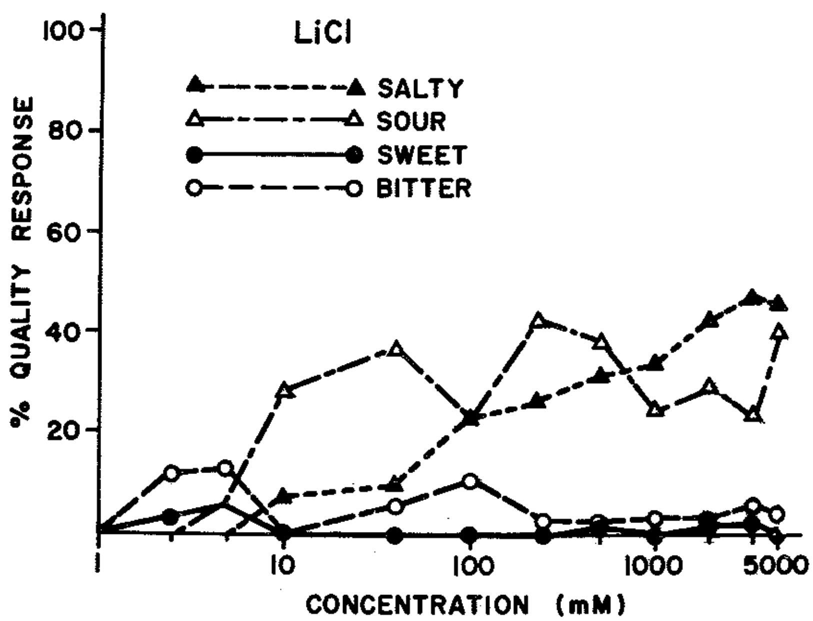

Fig.5 Percentage of each quality response as a function of concentration of LiCl.

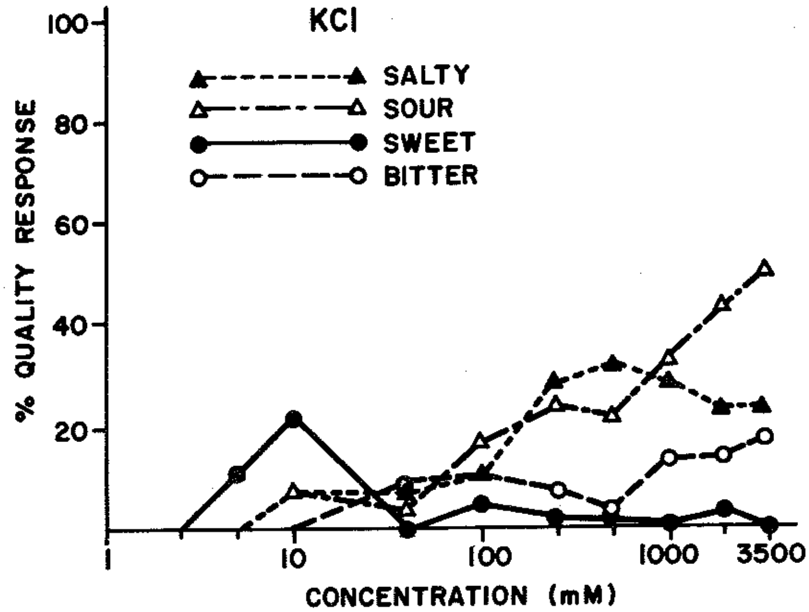

Fig.6 Percentage of each quality response as a function of concentration of KCl.

is simultaneously present. At higher concentrations there is an increase in both sour and salty responses, so that, for LiCl, the predominant taste in the mid-concentration range is sour. At the highest concentrations, NaCl and LiCl assume their characteristic salty taste, while KCl acquires a strong sour taste, with some salty and bitter also present.

Discussion

Sour-salty confusion. The above taste quality changes as a function of concentration are similar to those observed with whole-mouth procedures (Dzendolet & Meiselman, 1967a; Cardello & Murphy, 1977), although the sour component at higher concentrations of each salt is greater than has been previously reported. This finding is consistent with the results of Experiment II, in which it was found that the percentage of sour responses to NaCl were greater at higher salt concentrations (Figures 2 and 3). A similar correspondence between the single papilla data and the dorsal tongue data was observed for the acids. Of 200 single-papilla quality responses to HCl, 60% were sour, 30% were salty, 2% were sweet and 8% were bitter. For citric acid the percentages were identical. The 30% salty responses in these single papilla data are approximately the same as was found to HCl in Experiment II (Fig. 2). Taken together, these data suggest a common mechanism(s) underlying the sour-salty confusion in the dorsal tongue data of Experiments I and II and that affecting the single papilla responses in Experiment III.

The sour-salty confusion found in both the single papilla data and the data involving small-area stimulation of the dorsal tongue is important for a number of reasons. First, McCutcheon and Saunders (1972), in their work on chemical stimulation of single papillae were unable to find consistent salty responses to NaCl. They reported that:

> Sodium chloride gave stable "sour" responses in one papilla for both subjects. Although the two subjects occasionally gave "salty" responses to sodium chloride stimulation, the predominant response was "sour"... Our failure to obtain the reliable "salty" responses to a strong concentration of NaCl is perplexing. It is possible that simultaneous stimulation of several papillae will be necessary to obtain a clear "salty" response. (McCutcheon & Saunders, 1972, (p.216)).

The "perplexing" phenomenon that McCutcheon and Saunders reported, appears to be a reproducible aspect of human taste quality discrimination under conditions of small-area dorsal tongue stimulation. Furthermore, their suggestion that stimulation of several papillae may be necessary to obtain stable "salty" responses must be expanded as a result of Experiments I and II, since in these experiments a large number of papillae were stimulated simultaneously, yet the confusion was still present. In addition to the "sour" responses to NaCl, McCutcheon and Saunders (1972) reported numerous "salty" responses to stimulation with HCl. As with the present data, these responses support the existence of a sour-salty taste confusion. The existence of a sour-salty confusion may also account for some of the "inappropriate" quality responses reported by Harper, *et al.* (1966) during single papilla stimulation and by Collings (1973) during small area dorsal tongue stimulation with saturated filter paper.

Mechanism of taste quality changes. Although the present single papilla data for the three salts are characterized by a much larger sour component at higher concentrations than has been found with whole mouth procedures, if this sour component is ignored, the remainder of the quality data in Figs. 4 - 6 are almost identical to the whole mouth data as reported by Dzendolet and Meiselman (1967) and Cardello and Murphy (1977). Specifically, the sweet quality predominates at the lowest concentrations of NaCl and LiCl and is present to some appreciable degree only up to 10 - 50 mM for the three salts. Both Dzendolet and Meiselman (1967) and Cardello and Murphy (1977) reported the sweet quality to predominate at the lowest concentrations of these salts and to be present in some degree up to 20 - 50 mM. Thus, although the threshold for salt stimulation is higher for single papillae than for the whole mouth due to areal summation, the taste quality that is elicited from papillae with sufficiently low thresholds by low concentration salts is predominantly sweet. Similary, in agreement with the data of Dzendolet and Meiselman (1967) and Cardello and Murphy (1977), the present data show the salty quality to first emerge at about 10 mM and to continue to increase throughout the greater portion of the concentration range of these salts. The bitter quality, which never totaled more than 10 - 15% of responses in this study, except at the highest concentrations of KCl, was also never observed to predominate at any but high KCl concentration in the studies by Dzendolet and Meiselman (1967) and Cardello and Murphy (1977).

The above correspondence between the taste quality changes occuring within single papillae and those reported for the whole mouth supports Dzendolet's (1968) hypothesis that concentration-dependent physicochemical changes in these salts are responsible for the observed taste qualities. Such a conclusion is based on the fact that if such physicochemical changes produce structures in the solutions that affect different receptor types, these structures must also be present in solutions presented to a single papilla and would be expected to produce similar concentration-dependent quality changes.

However, at the same time that these data support Dzendolet's physicochemical hypothesis, they disaffirm his proposed inhibitory mechanism by which one quality replaces another. Dzendolet proposed that this inhibition occurs between individual, quality-specific papillae. Since only one papilla was stimulated on each trial in this experiment, Dzendolet's inhibitory mechanism cannot serve as an explanation of the observed quality changes with concentration. Thus, a modification of Dzendolet's theory is necessary. Such a modification may involve inhibition that occurs between either individual taste buds or individual receptor cells. However, in lieu of supporting neural data, it is expedient to reserve further speculation on the nature of this inhibitory mechanism, and to, instead, focus future research on the theory's specific predictions of quality-intensity relationships for various ionic series of halide salts.

Acknowledgment

The author wishes to express his deepest appreciation to Dr. Ernest Dzendolet for his help and guidance during the conduct of this research.

References

Abrahams, H., Krakauer, D. and Dallenbach, K. Gustatory adaptation to salt. *Am. J. Psychol.*, 1937, **49**, 462-469.

Bealer, S.L. and Smith, D.V. Multiple sensitivity to chemical stimuli in single human taste papillae. *Physiol. & Behav.*, 1975, **14**, pp. 795-799.

Bekesy, G. von Sweetness produced electrically on the tongue and its relation to taste and theories. *J. Appl. Physiol.*, 1964, **19**, pp. 1105-1113.

Bekesy, G. von Duplexity theory of taste. *Science*, 1964b, **145**, pp. 834-835.

Bekesy, G. von Temperature coefficients of the electrical thresholds of taste sensations. *J. Gen. Psych.* 1965, **49**, pp. 27-35.

Collings, V.B. Human taste response as a function of locus of stimulation on the tongue and soft palate: implications for sensory coding. Ph.D. Dissertation, University of Pittsburg, 1973.

Cardello, A.V. Chemical stimulation of single human fungiform taste papillae: Sensitivity profiles and locus of stimulation. *Sensory Processes*, 1978, **2**, 173-190.

Cardello, A.V. and Murphy, C. Magnitude estimates of gustatory quality changes as a function of solution concentration of simple salts. *Chem. Senses & Flavor*, 1977, **2**, pp. 327-341.

Dzendolet, E. A structure common to sweet-evoking compounds. *Percept. & Psychophys.*, 1968, **3**, pp. 65-68.

Dzendolet, E. and Meiselman, H. Cation and naion contributions to gustatory quality of simple salts. *Percept. & Psychophys.*, 1967, **2**, pp. 601-604.

Gregson, R.A.M. and Baker, A.F.H. Sourness and bitterness: Confusions over sequences of taste judgements. *Br. J. Psychol.*, 1973, **64**, pp. 71-76.

Harned, H. and Owen, B. *The physical chemistry of electrolytic solutions.* (2nd ed.) New York: Reinhold, 1950).

Harper, H., Jay, J., and Erickson, R. Chemically evoked sensations from single human taste papillae. *Physiol. & Behav.*, 1966, **1**, pp. 319-325.

Hober, R. and Kiesow, F. Ueber den Geschmack von Salzen und Laugen. *Z. Physikal. Chemie*, 1898, **27**, pp. 601-616.

Holway, A. and Hurvich, L. Differential gustatory sensitivity to salt. *Am. J. Psychol.*, 1937, **49**, 37-48.

Hunt, D., DuBose, C. and Meiselman, H.L. The contribution of stinging to the sodium chloride taste sensation. Unpublished manuscript, 1978.

McAuliffe, W.K. and Meiselman, H.L. The roles of practice and correction in the categorization of sour and bitter taste qualities. *Percept. & Psychophys.*, 1974, **16**, pp. 242-244.

McBurney, D. Effects of adaptation on human taste functions. IN: *Olfaction and Taste*. C. Pfaffmann, (Ed.), New York: Rockefeller Press, 1969.

McBurney, D. and Bartoshuk, L. Interactions between stimuli with different taste qualities. *Physiol & Behav.*, 1973, **10**, 1101-1106.

McCutcheon, N.B. and Saunders, J. Human taste papilla stimulation: stability of quality judgments over time. *Science*, 1972, **175**, pp. 214-216.

McFadden, H.B. The influence of temperature and solution concentration on reaction time to taste stimuli (sodium chloride). *J. Psychol.*, 1937, **4**, 349-363.

Meiselman, H.L. and Dzendolet, E. Variability in gustatory quality identification, *Percept. & Psychophys.*, 1967, **2**, pp. 496-498.

Moncrieff, R.W. *The Chemical Senses*, London: Leonard Hill, 1967.

O'Mahony, M. Qualitative description of low concentration sodium chloride solutions, *Br. J. Psychol.*, 1973, **64**, 601-606.

O'Mahony, M. and Godman, L. The effect of interstimulus procedures on salt taste thresholds. *Percept. & Psychophys.*, 1974, **16**, 459-465.

Renqvist, Y. Uever den Geschmack, *Skand. Arch. Physiol.*, 1919, **38**, pp. 97-201.

Robinson, F.O. The misuse of taste names by untrained observers. *Br. J. Psychol.*, 1970, **61**, pp. 375-379.

Skramlik, E. von *Handbuch der physiologie der Niederen Sinne*. Leipzig: George Thieme, 1926, Partial translation by G.R. Schaub, 1967.